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Genetic correlation between temperature-induced plasticity of life-history traits in a soil arthropod

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Abstract Temperature is considered one of the most important mediators of phenotypic plasticity in ectotherms. However, the costs and benefits shaping the evolution of different thermal responses are poorly elucidated. One of the possible constraints to phenotypic plasticity is its intrinsic genetic cost, such as genetic linkage or pleiotropy. Genetic coupling of the thermal response curves for different life history traits may significantly affect the evolution of thermal sensitivity in thermally fluctuating environments. We used the collembolan *Orchesella cincta* to study if there is genetic variation in temperature-induced phenotypic plasticity in life history traits, and if the degree of temperature-induced plasticity is correlated across traits. Egg development rate, juvenile growth rate and egg size of 19 inbred isofemale lines were measured at two temperatures. Our results show that temperature was a highly significant factor for all three traits. Egg development rate and juvenile growth rate increased with increasing temperature, while egg size decreased. Line by temperature interaction was significant for all traits tested; indicating that genetic variation for temperature-induced plasticity existed. The degree of plasticity was significantly positively correlated between egg development rate and growth rate, but plasticity in egg size was not correlated to the other two plasticity traits. The findings suggest that the thermal plasticities of egg development rate and growth rate are partly under the control of the same genes or genetic regions. Hence, evolution of the thermal plasticity of traits cannot be understood in isolation of the response of other traits. If traits have similar and additive effects on fitness, genetic coupling between these traits may well facilitate the evolution of optimal phenotypes. However, for this we need to know the selective forces under field conditions.

Keywords Phenotypic plasticity · Temperature reaction norm · Egg development · Juvenile growth · Egg size · Collembola

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Introduction

Temperature is a key environmental factor for ectotherms and affects a large number of life history traits. The value that a trait assumes under different temperature conditions is described by a thermal reaction norm. The degree of plasticity is defined as the slope of a reaction norm, i.e., a steeper relationship is considered to be more plastic (de Jong 1990). A large number of laboratory experiments and quantitative genetic studies have demonstrated that there is genetic variation among individuals and populations in the steepness and elevation of thermal reaction norms (Loeschcke et al. 1999; Steigenga et al. 2005; Driessen et al. 2007; Gutteling et al. 2007; van Asch et al. 2007; Liefing and Ellers 2008; Bahrndorff et al. 2009). Such variation is possibly caused by biochemical differences in metabolic enzymes (Hochachka and Somero 2002) or by differences in gene expression (Schlichting and Smith 2002; Li et al. 2006; Ellers et al. 2008).

However, the selective pressures driving the evolution of different thermal responses are not yet elucidated. Several studies implicate natural selection in population differences in temperature-induced plasticity (or canalization) (Orizaola and Laurila 2009; Liefing et al. 2009; Terblanche and Kleyhans 2009). Recently, the idea has been put forward that one of the possible constraints to phenotypic plasticity is its intrinsic genetic cost, such as genetic linkage or pleiotropy (De Witt et al. 1998; Van Kleunen and Fischer 2007). Plastic traits do not evolve in isolation of other traits, and selection on the degree of plasticity in one trait may produce a response in many other traits, including the degree of plasticity of other traits. Genetic linkage between the plasticity of traits may constrain the development of an optimal phenotype (Schlichting and Pigliucci 1998; Pigliucci and Kaplan 2000; Beldade et al. 2002; Ellers and Boggs 2004). That is, the fitness benefits of a strong plastic response in one trait, may be offset by a correlated response in the plasticity of other traits. Vice versa, if two correlated traits have similar and additive effects on fitness, a genetic correlation between those traits may actually facilitate the evolution of optimal phenotypes.

Genetic correlations are commonly found for traits in constant environments (Beldade et al. 2002; Allen et al. 2008), but thus far, relatively few studies have looked for genetic correlations between environmentally-induced changes in traits. For example, *Arabidopsis thaliana* genotypes showing the strongest flowering delay in response to vernalization treatment generally also show the largest increase in leaf number at flowering (Callahan et al. 2005). On the other hand, thermally-induced changes in wing coloration are uncoupled in butterflies (Brakefield et al. 1998; Ellers and Boggs 2004), as well as predator-induced responses in behavioural, life-history and morphological traits in *Daphnia pulex* (Boersma et al. 1998; Boeing et al. 2006). In these cases, the degree of plasticity of different traits can respond independently to natural selection. The presence of genetic correlations between traits is thought to result from shared regulatory pathways that constrain independent evolution of traits (Weinig et al. 2006; Allen et al. 2008). The strength of thermal responses of many life history traits such as growth rate, development time and locomotory behaviour, depends critically on temperature-induced changes in metabolic rate (Brown et al. 2004). Therefore, we hypothesize that a shared dependence on metabolic rate causes genetic correlations among the thermal responses of different life history traits. This would imply that the fitness consequences of temperature-induced plasticity may also depend on correlated thermal responses in other characters.

Here, we want to investigate the evolutionary genetics of temperature-induced plasticity, in particular the presence of genetic correlations between thermal responses of life history traits. Our model organism is the springtail *Orchesella cincta* (L.), a soil arthropod found in a wide variety of habitats in the Holarctic (Timmermans et al. 2005a). Springtails

are a globally significant group of organisms that play a major role in ecosystem functioning (Rusek 1998). Earlier studies have shown that *O. cincta* is adapted to local conditions including temperature (Timmermans et al. 2005b; Bahrndorff et al. 2006), and shows significant variation in temperature-induced plasticity of life history traits (Ellers et al. 2008; Liefting and Ellers 2008).

A major selection pressure in the field is predation of egg and juvenile stages of *O. cincta* (Van Straalen 1985); hence, thermal responses of life history traits should evolve together to reduce time to first reproduction. Obviously, egg development rate and juvenile growth rate are the main determinants of egg-to-adult development time, but egg size can also reduce the time to reach maturity because large eggs are generally assumed to have a shorter development time than small eggs (Fox 1994). In addition, large eggs generally give rise to larger progeny in arthropods (Fox and Czesak 2000), which may reach maturity faster. Like many insects, *O. cincta* shows thermal responsiveness in egg size so that smaller eggs are produced at higher temperatures (Liefting et al. 2010). We therefore expect to find plasticity for three life-history traits: egg development rate, egg size and juvenile growth rate.

In the present study we address two research questions: (1) Is there genetic variation in the plastic response of life history traits to temperature and (2) Is the degree of temperature-induced plasticity correlated across traits?

Methods and materials

Animals and experimental populations

Orchesella cincta (L.) is a soil-dwelling arthropod species (adult size 3–5 mm) distributed across Europe. It is found in the litter layer of forests, where it feeds on fungi and algae. The average annual density may reach up to 1,500 animals per m², but its abundance is highly variable between sites (van Straalen 1989). *O. cincta* is a sexually reproducing species with moderately high levels of genetic diversity found within populations (Timmermans et al. 2005a). We created 19 inbred isofemale lines to obtain individuals of nearly identical genotype required for the experiment. Using inbred lines is a common procedure to address questions concerning phenotypic plasticity (Callahan et al. 2005; Weinig et al. 2006). Each line was initiated by one parental pair from a laboratory culture that had been outbred in the laboratory for five generations (see Driessen et al. 2007 for details). In subsequent generations, population size of the inbred lines was increased to five individuals to reduce strong deleterious inbreeding effects. Lines were kept at 20°C, 70% humidity and a photoperiod of 12L:12D. Food consisted of pieces of bark overgrown with green algae (*Desmococcus* spec.) and was always kept in excess. At the start of the experiment the lines had gone through six generations of inbreeding. Because not all five individuals necessarily contributed to the next generation, effective population size may have varied among generations, leading to an estimated coefficient of inbreeding of at least 0.55 (Falconer 1989).

Experimental design and trait measurements

We measured the three life history traits for each isofemale line at two temperatures. Only two temperatures were used because thermal reaction norms are practically linear over this temperature range (Van Straalen and Joosse 1985; Stam 1997; Driessen et al. 2007).

Egg development rate and juvenile growth rate were measured at 12°C and 22°C, which is within the temperature range experienced by *O. cincta* in the field (Liefing and Ellers 2008). Egg size was measured at 16°C and 22°C because hardly any eggs are produced at 12°C. During all these treatments humidity in the climate chambers was 70% and the photoperiod 12L:12D.

At the start of the experiment nine pairs of young adult springtails (~ 600 µg) of each line were kept at 20°C in a small plastic container with a bottom of plaster of Paris and food, and inspected every morning for eggs. *O. cincta* starts laying eggs directly after the onset of light. When the first clutch of eggs was laid five randomly chosen eggs were incubated individually in separate containers at 12°C and checked daily for hatching. Five other randomly chosen eggs were similarly incubated at 22°C and checked twice a day for hatching. Egg development rate was calculated as the inverse of the time between laying and hatching. Juveniles emerging at 12°C were reared for 50–55 days (average wet weight: 261.1 (±94.3) µg) and those that had emerged at 22°C for 20–25 days (average wet weight: 449.4 (±178.3) µg). The different lengths of the growth period at low and high temperatures allowed us to measure both groups at approximately equal developmental stage. The wet weight was determined to the nearest 1 µg on a microbalance (Mettler Toledo UMT2). Growth of juvenile *O. cincta* is exponential (Janssen and Joosse 1987) and the initial juvenile weight after hatching (~ 5 µg) is negligible compared to the weight at the moment of measurement (average >350 µg). We therefore calculated the daily growth rate as the natural logarithm of the wet weight divided by the time between hatching and weighing (in days).

After a pair had laid its first clutch it was transferred to a climate room at 16°C. The pair was checked daily until the second clutch was laid. Ten randomly chosen eggs of this clutch were photographed using a digital camera (Leica DC200) connected to a stereomicroscope. The diameter of the eggs was measured to the nearest 0.02 mm using public software ImageJ 1.30v. Eggs of *O. cincta* are perfectly spherical and diameter is a good estimate of total egg mass (transformation of diameter to volume yields identical conclusions; we will only present results for diameter). Immediately after the second clutch was produced, the pair was transferred to 22°C to produce a third clutch of which ten randomly chosen eggs were measured as described above. Although this design confounds clutch rank order with temperature (the last clutch was always laid at the higher temperature), we were confined to this design because continuous 22°C is rather high for *O. cincta*, and reversing the temperature order might have lead to premature death of pairs. However, a previous study showed that egg size of *O. cincta* females does not change between two consecutive clutches at 20°C (Zizzari et al. 2009). Our total dataset contained data from 97 pairs for egg development rate (516 individuals), from 92 pairs for juvenile growth rate (416 individuals) and from 69 pairs for egg size (1,329 eggs).

Statistical analysis

Genetic variation

We used General Linear Models (GLM) to test for the fixed effect of temperature, line, and temperature × line, and the random effects of pair nested within line on phenotypic traits. A significant temperature effect indicates that springtails respond plastically to temperature, while a significant line × temperature interaction demonstrates that lines differ in plasticity. The pair term effectively controls for parental effects.

Development rate and growth rate failed to meet the assumption of equal variances. Natural logarithm and square root transformation improved homoscedasticity of

development rate and juvenile growth rate, respectively, and the GLM results are reported for the transformed data. In neither case did the significance tests differ between raw and transformed data. We therefore present means (Fig. 1; Table 1) for the untransformed data.

Genetic correlation within and between temperatures

To explore the relationship between different life history traits, we tested for correlations within and between temperatures. For each line, trait means were calculated per temperature. Plasticity was calculated for each trait as the difference in line means at the two temperature treatments (trait mean at 22°C minus trait mean at 12°C), divided by the difference in

Fig. 1 Thermal reaction norms of egg development rate (**a**), juvenile growth rate (**b**) and egg size (**c**) for 19 isofemale lines of *Orchesella cincta*

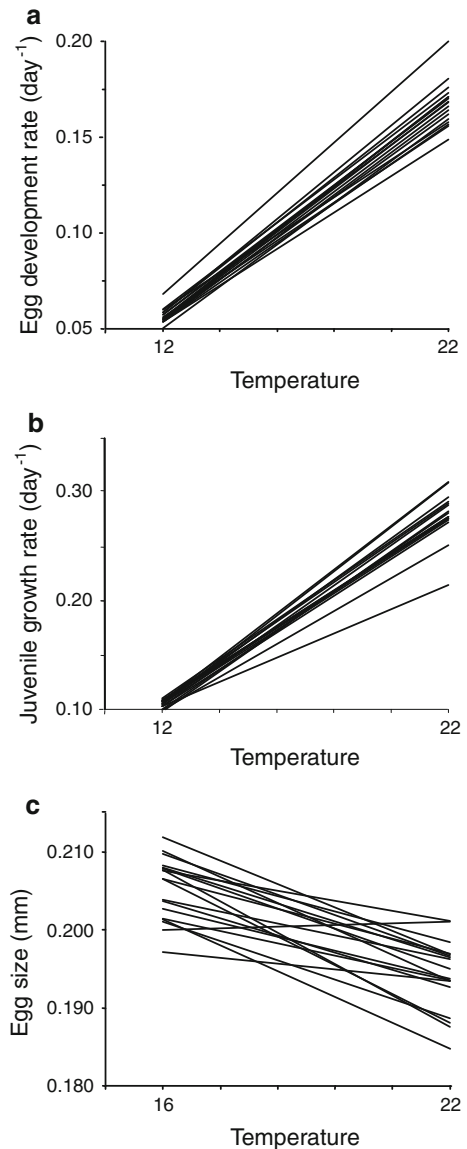


Table 1 Results of GLM (*F*-ratios) testing for the effect of temperature and line on egg development, egg size and juvenile growth rate of 19 isofemale lines of *Orchesella cincta*

Source	Pair (IFL)	IFL	Temperature	IFL \times temp	Trait means \pm 1 SE	
					12°C	22°C
Egg dev rate	5.45***	2.33**	16,100***	1.84*	0.056 \pm 0.0003 ^A	0.168 \pm 0.0009 ^B
Growth rate	1.90***	2.54**	5,036.2***	3.56***	0.1045 \pm 0.0009 ^A	0.2848 \pm 0.0018 ^B
Egg size (mm)	7.97***	0.97	293.6***	4.04***	0.205 \pm 0.0003 ^A	0.195 \pm 0.0003 ^B

Pair was included in the model to control for parental effects. Bold values indicate significant fixed factors. The right two columns present the treatment means (\pm 1 SE) for all traits with significant differences indicated by lettered superscripts

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

temperature. We use means based on the untransformed data to preserve similar scale among life-history traits. Normality assumptions were met for all trait means and plasticity values. Pearson's product correlations were estimated between trait means at each of the two temperatures, and between plasticities for the different traits. The trait means and plasticity were weighted by the sample size contributing to each value. The critical probability levels for the correlation coefficients were Bonferroni corrected for multiple comparisons to $\alpha/3 = 0.016$. All statistical analyses were carried out in SPSS, version 14.0.

Results

Genetic variation for phenotypic plasticity

Average egg development rate, juvenile growth rate and egg size differed significantly between the two temperature treatments (Table 1; Fig. 1). On average, eggs were smaller and developed faster at high compared to low temperature. Also, individuals had a higher growth rate at high temperature. Temperature was a highly significant factor in the GLM analysis for all three traits (Table 1). The factor pair contributed significantly to all models, suggesting that maternal or paternal effects affected offspring life history, even within isofemale lines. Lines differed significantly in the average trait values for egg development rate and juvenile growth rate, but not egg size (Table 1). Most importantly, the interaction between line \times temperature was significant for all traits tested (Table 1; Fig. 1), indicating that genetic variation for temperature-induced plasticity existed. Figure 1 depicts the mean reaction norms for all lines. Differences in the slope of the reaction norms among lines were in the magnitude of the effect rather than the direction of plasticity (i.e., sign of the slope). For egg size, one line showed a reverse pattern of plasticity with larger eggs at higher temperature, but this effect was only small.

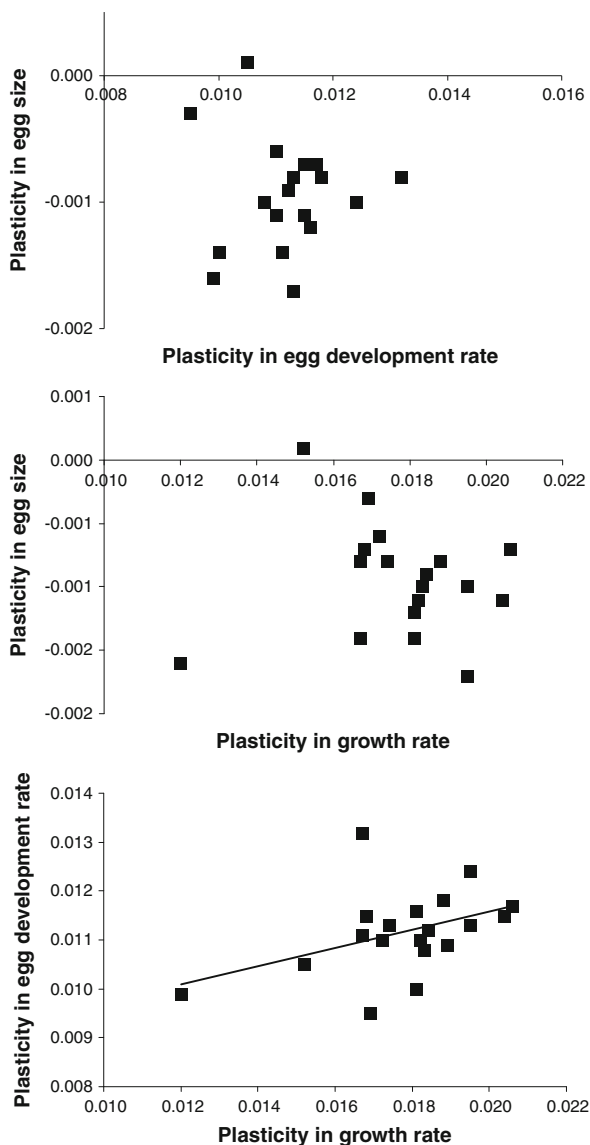
Genetic correlations between the levels of phenotypic plasticity

We did not detect any significant genetic correlations among the life history traits under either low or high temperature conditions (Table 2, above and below the diagonal). In contrast, a significant positive relationship was observed between the degree of plasticity in egg development rate and growth rate ($r = 0.573$, $N = 19$, $P = 0.010$). Lines that showed a strong increase in growth rate with temperature, generally also showed a strong temperature-induced increase in egg development rate (Fig. 2). No genetic correlations were found in the

Table 2 Genetic correlation matrix of life history traits of 19 isofemale lines of *Orchesella cincta* exposed to low temperature (above diagonal) and high temperature (below diagonal)

	Egg dev. rate	Growth rate	Egg size
Egg dev rate	–	0.122 ($n = 19$)	–0.240 ($n = 18$)
Growth rate	0.282 ($n = 19$)	–	0.034 ($n = 18$)
Egg size	0.204 ($n = 18$)	–0.024 ($n = 18$)	–

The table shows correlation coefficients and sample size. Low temperature was 12°C to measure egg development rate and juvenile growth rate, and 16°C to measure egg size; high temperature was 22°C for all traits. None of the correlation coefficients were significantly different from 0 ($P > 0.05$)

Fig. 2 Genetic correlations between the slopes of the thermal reaction norms for egg development rate, juvenile growth rate, and egg size of 19 isofemale lines of *Orchesella cincta* reared at two temperatures

degree of plasticity between egg size and egg development rate ($r = -0.088$, $N = 18$, $P = 0.721$) nor between egg size and growth rate ($r = -0.101$, $N = 18$, $P = 0.681$; Fig. 2).

Discussion

Our results demonstrate significant temperature-induced genotype-by-environment interaction for all three life history traits we studied in *O. cincta*. The presence of genetic variation for phenotypic plasticity supports the growing consensus that phenotypic plasticity itself is a genetic trait (Scheiner 1993; Scheiner and Yampolsky 1998) and that the reaction norm approach provides a valuable approach to studying its genetics (Loeschcke et al. 1999; Steigenga et al. 2005; Gutteling et al. 2007). Genetic variation for temperature response has been reported for several species (Hassall et al. 2006; Seko et al. 2006; Gutteling et al. 2007), but seems to be lacking in others (Fischer et al. 2004; Azevedo et al. 1996). Possible reasons for these contradictory results may lie in the specific trait under study or the experimental approach used to detect genetic variation in plasticity (Callahan et al. 2005; van Kleunen and Fischer 2007; Dechaine et al. 2007). Alternatively, the evolutionary history of study populations may have led to genetic erosion of variation for plasticity through bottlenecks or strong directional selection. Unfortunately, general theory to understand the selective pressures maintaining genetic diversity for phenotypic plasticity is lacking so far.

Furthermore, it remains largely unknown how much of the genetic variation for phenotypic plasticity is additive, and thus amenable to selection. Several experiments documented limited direct responses to selection on plasticity (Scheiner et al. 1991; Wijngaarden and Brakefield 2001; van Kleunen et al. 2002; Callahan and Pigliucci 2005; Driessen et al. 2007) which may reflect the existence of considerable non-additive variation for the slope of the reaction norm. Nevertheless, differentiation of life history reaction norms is frequently observed in the field, for example in thermally divergent habitats of *O. cincta* (Liefting and Ellers 2008; Bahrndorff et al. 2009) as well as for other species (Hassall et al. 2006; Liefting et al. 2009). Population differentiation with respect to the level of plasticity can be found at microgeographic scale (Orizaola and Laurila 2009) and is even maintained in the face of gene flow (Liefting 2009). This strongly suggests that the level of phenotypic plasticity readily responds to selection under natural conditions. Further study is required to understand the genetic architecture of evolved population differences in the degree of phenotypic plasticity.

We expected genetic correlations among the thermal responses for egg development rate, egg size and juvenile growth rate because they are all largely determined by the extent of temperature-induced changes in metabolic rate and act together to pass the animals through the most vulnerable stages of their development. Indeed we found a genetic correlation between the thermal response of egg development rate and juvenile growth rate which suggests that part of the genes that determine the reaction norm for egg development rate are also involved in shaping the reaction norm for juvenile growth rate. The exact details of the genetic architecture underlying phenotypic plasticity are still unknown, but several quantitative trait loci (QTL's) have been identified that are associated with temperature-induced plasticity in life history traits (Gutteling et al. 2007). Overlapping QTL's such as those found in *Caenorhabditis elegans* for thermal sensitivity of growth rate and age at maturity may be indicative to shared control of these traits (Gutteling et al. 2007). The fact that we found a genetic correlation between plasticity levels which was well

below unity implies that other, more down-stream acting genes may also be involved, and that independent evolution is possible.

The thermal response of egg size was not correlated with the thermal response of any of the two other traits. The response of egg size to temperature followed the general temperature-size rule (Atkinson 1994): eggs were smaller at higher temperature. A limitation of our design was that the effects of temperature and clutch rank were confounded because the last clutch was always laid at the higher temperature. In many insects progeny size decreases with age (Fox and Czesak 2000), so that later clutches are expected to contain smaller offspring. However, in *O. cincta* it has been shown that the egg size does not change between two consecutive clutches (Zizzari et al. 2009), perhaps because Collembola females continue to grow after the onset of reproduction. As a result, our estimates for the magnitude of temperature-induced egg size plasticity will not be affected by female age nor will our conclusions concerning genetic variation in thermal sensitivity of egg size.

The observed lack of genetic coupling among thermal response of egg size and the thermal responses of egg development rate and juvenile growth rate suggests that the thermal sensitivity of egg size is limited by a different developmental process than the other two life history traits. Alternatively, we may have erroneously assumed egg size to be involved in the time to reach maturity in *O. cincta*. Large eggs are generally assumed to have a shorter development time than small eggs (Fox 1994), but this relationship is ambiguous as several studies have reported longer development times for larger eggs (Ernsting and Isaaks 1997; Sinervo 1990). In another study on *O. cincta* the effect of egg size on development rate was itself temperature-dependent: large eggs only show a higher development rate than small eggs at high rearing temperatures, not at low rearing temperatures (Liefting et al. 2010). Apart from being related to egg development time, large egg size has also been reported to enhance egg survival under stressful conditions (Fox and Czesak 2000; Liefting et al. 2010). If egg size in *O. cincta* is most important for hatching success, an uncoupling with plasticity of egg development rate and juvenile growth rate could facilitate the evolution of optimal egg size plasticity with respect to egg survival.

Studies on thermal sensitivity of traits are particularly well-suited to identify constraints and benefits of multi-trait evolution. The thermal environment at any one time is always imposed on the whole organism and consequently on many traits simultaneously. The ultimate performance of an organism is thus the joint result of a collection of reaction norms. Whether genetic correlations are constraining evolution or not, depends on the life histories of the organisms involved. If two or more traits have similar and additive effects on the same fitness parameter, genetic coupling between these traits as found in this study may well facilitate the evolution of optimal phenotypes.

The genetic architecture underlying the genetic correlation determines the probability of selection producing correlated responses (Czesak et al. 2006). Thus, the interpretation of genetic correlations has to be placed in a broader context; and for this we need to know the selective forces under field conditions. In general, there is a growing appreciation of the adaptive importance of thermal plasticity for life-history traits in ectotherms, for instance in coping with the consequences of global warming and invasive species (Richards et al. 2006; Chown et al. 2007; Berg et al. 2010). This study has shown that genetic correlations between thermal sensitivities of life history traits exist, and this could facilitate the adaptation to the local thermal environment.

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